
Past and Distant Whaling and the Rapid Decline of Sperm Whales off the Galápagos Islands

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Abstract: *It is generally expected that exploited whale populations should rebuild following the end of whaling. Using photographic identification of individuals during a series of field projects, we studied female and immature sperm whales (*Physeter macrocephalus*) that visit the waters off the Galápagos Islands, Ecuador. Analysis of mark-recapture data, using a likelihood model, indicates the population decreased at a rate of about 20% per year (95% c.i. 7-32%) between 1985-1995. During the study period the animals were not hunted and were not obviously the subject of other immediate anthropogenic threats. Rates at which research vessels encountered whales also fell over this interval. The decline seems to be due principally to migration into waters off the Central and South American mainland. The population also has a very low recruitment rate, about 0.05 calves/female/year, as indicated by rates of observation of calves. Although other causes cannot be ruled out, both the high emigration rate and low recruitment rate are probably related to heavy whaling in Peruvian waters which ended in 1981. Whales from the Galápagos are moving east to fill productive but depopulated waters near the coast, and the virtual elimination of large breeding males (in their late twenties and older) from the region has lowered pregnancy rates. The case of the Galápagos sperm whales strongly suggests that exploitation can continue to have substantial negative impacts on the size and recruitment rate of an animal population well outside the range of the hunt and for at least a decade after it has ended.*

Explotación en el Pasado y la Rápida Declinación de los Cachalotes de las Islas Galápagos

Resumen: *Generalmente se espera que las poblaciones de ballenas que han sido explotadas se recuperen al término del período de explotación. Por medio de identificación fotográfica de individuos estudiamos hembras e inmaduros de cachalotes (*Physeter macrocephalus*) que visitan las aguas cercanas a las Islas Galápagos, Ecuador. El análisis de datos de captura-recaptura, utilizando un modelo de probabilidad, indica que la población declinó a una tasa aproximada de 20% por año (95% c.i. 7-32%) entre 1985 y 1995. Durante el estudio los animales no fueron cazados ni estuvieron sujetos a otras amenazas antropogénicas inmediatas y obvias. Durante este intervalo también decrecieron las tasas de avistamiento de ballenas desde barcos de investigación. La declinación parece deberse principalmente a la migración hacia aguas cercanas a la costa de Centro y Sudamérica. La observación de crías indica que la población también tiene una tasa de reclutamiento muy baja, aproximadamente 0.5 crías/hembra/año. Aunque no se pueden descartar otras causas, tanto la elevada tasa de emigración como la baja tasa de reclutamiento probablemente se deben a la cacería intensiva en aguas peruanas que terminó en 1981. Ballenas de las Galápagos se están moviendo hacia el este para ocupar aguas productivas pero despobladas cercanas a la costa y la eliminación virtual de machos reproductores (de 20 años o más) ha reducido la tasa de reproducción. El caso de los cachalotes de las Galápagos sugiere que la cacería puede causar impactos negativos significativos sobre el tamaño y la tasa de reclutamiento de una población animal fuera del área de caza y por lo menos una década después de terminada la cacería.*

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Introduction

During the 20th century, most populations of large whales were severely depleted by whaling. Beginning in the 1930s, the most seriously affected were given protection, and in 1986 the International Whaling Commission instituted a moratorium on commercial whaling. With protection, populations were expected to rebuild. Recovery has been observed in some cases, including populations of the southern right whale (*Eubalaena australis*) (e.g., Payne et al. 1990) and the eastern Pacific gray whale (*Eschrichtius robustus*) (Buckland et al. 1993). There are, however, protected populations, such as the northern right whale (*Eubalaena glacialis*), that show few signs of recovery, probably because of anthropogenic threats including by-catch in fisheries and collisions with ships (Brown et al. 1995).

It is important to monitor the performance of protected populations. If they fail to recover as anticipated after the removal of the principal perceived threat, then either there are additional threats affecting the population, perhaps originating outside the study area, or the effects of the original threat linger. Spatial effects and temporal lags in the results of anthropogenic disturbance are vital considerations in conservation biology (e.g., Tilman et al. 1994; Kareiva & Wennergren 1995). We examined a protected population of sperm whales that is declining rapidly and relate the decline to past and distant whaling.

The sperm whale (*Physeter macrocephalus*) is a large, sexually dimorphic (ca 15 t for adult females, 45 t for adult males) odontocete found throughout deeper waters of the world's oceans (Rice 1989). It was a primary target for whalers from the 18th century until the 1970s, with hundreds of thousands killed (Gosho et al. 1984). There is no published information on trends in sperm whale populations following the end of whaling, with the exception of an apparent increase in the numbers of males in Antarctic waters during the 1980s indicated by the preliminary analysis of Butterworth et al. (1995).

The waters off the Galápagos Islands, Ecuador, have been an important habitat for sperm whales for at least two centuries (Colnett 1798; Shuster 1983; Wade & Gerrodette 1993). Galápagos sperm whales were exploited heavily by open-boat whalers during the first half of the 19th century (Shuster 1983): about 5000 animals were removed from the waters close to the islands between 1830–1850, and during this period the population showed signs of depletion (Hope & Whitehead 1991). There are no records of modern whalers working near the islands, although heavy sperm whaling took place off Peru (≥ 1000 km to the east-southeast, Fig. 1) between 1957 and 1981 (e.g., Ramirez 1989). Marked and photo-identified sperm whales have traveled from the Galápagos to waters in and near the Peruvian whaling grounds (Ivashin 1978; Dufault & Whitehead 1995b).

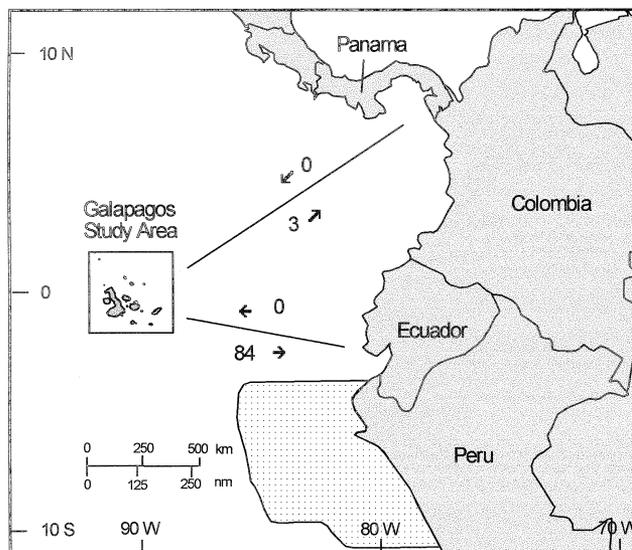


Figure 1. Study area off Galápagos Islands with sperm whale photo-identification matches to other areas in the eastern, tropical Pacific, and extent of whaling grounds off Peru (from Ramirez 1989).

We have studied the Galápagos sperm whales since 1985 using photo-identification and other methods (e.g., Whitehead 1990) and have made studies in other parts of the South Pacific (Dufault & Whitehead 1995b). Currently 1370 females and immatures have been identified from high quality photographs taken in Galápagos waters; mature males are rare, peaking at about 4% of the population in April (Whitehead 1993).

We show that the population of females and immatures that uses the Galápagos has declined substantially since 1985 and has an abnormally low recruitment rate.

Methods

Definitions

Our study area was in the waters near the Galápagos Islands bounded by 1°30' S–1°30' N; 89°–92°30' W.

We call all sperm whales, except for first-year calves (<ca. 5.5 m) and large (>ca. 12 m) males, "females and immatures." As the birth season (principally June–July; Whitehead et al. 1989) is largely outside the months in which our studies were carried out (Table 1) and intermediate sized males are not common in Galápagos waters (Waters & Whitehead 1990), first-year calves and large males were generally distinct and easily distinguishable.

The "Galápagos population" is defined to include all females and immatures that visited our Galápagos study area one or more times within intervals of about 2 years. Females and immatures generally spent a few days in the study area at any time (Whitehead 1996). Female and imma-

Table 1. Identifications of sperm whales off the Galápagos Islands and the nearby mainland of South and central America.

Dates	Area	Photographic identifications ^a	Distinct animals identified ^b
Feb 85	Ecuador	7	3
Feb 85–Apr 85	Galápagos	633	284
Jan 87–June 87	Galápagos	1095	370
Apr 88	Galápagos	250	82 ^c
Oct 88–Apr 89	Galápagos	613	348
Apr 89–June 89	Galápagos	843	293
Jan 91–Mar 91	Ecuador	426	239
Mar 91–Apr 91	Galápagos	113	72
June 92	Ecuador	4	4
June 92	Galápagos	0	0
Feb 93	Galápagos	18	16 ^d
Apr 93	Ecuador/Peru	182	91
Jan 94–June 94	Galápagos	32	22 ^d
Apr 95–June 95	Galápagos	140	53
June 95	Gulf of Panama	10	9

^aHigh quality ($Q \geq 4$) photographic identifications of female and immature sperm whales.

^bNumber of different animals identified during the study.

^cCourtesy of T. Lyrholm, vessel Siben.

^dCourtesy of G. Merlen, vessel Ratty.

ture sperm whales travel in permanent units of about 2–20 animals between which there is very little transfer (Whitehead et al. 1991). “Permanent units” generally consist of one, or possibly a few, matriline (Richard et al. 1996).

Field and Identification Techniques

Sperm whales were studied off the Galápagos Islands, and in other parts of the eastern tropical Pacific, during a number of field projects between 1985–1995 aboard 10- to 20-m research vessels (Table 1). For a subset of the field studies (those carried out by HW using standard acoustic and visual techniques to find whales) we noted the time spent searching over deep (>1000 m) water before each encounter with sperm whales.

Animals were identified individually from photographs of their tail-flukes (Arnbom 1987). We also noted whether the photograph was of a large male or a first-year calf and the number of first-year calves, large males, and other individuals in the cluster (whales swimming together) from which the photograph was taken.

Identification photographs from all studies and areas were processed and matched using the methods of Arnbom (1987) and Dufault and Whitehead (1995a). Each photograph was given a “Q” value from 0–5, based upon the quality of the image (not the quality of the marks) (Arnbom 1987). Only photographs with $Q \geq 4$ of females and immatures were used in the analysis.

Population Analysis

The size, and other parameters, of the Galápagos population were estimated using a likelihood mark-recapture

method conditioning on first identification, using calendar years as sampling units (with samples in November and December 1988 allocated to 1989). The model used has three parameters: an instantaneous rate of population increase of r /year; an instantaneous rate of mortality/emigration/mark-change (rate at which marked animals leave the identifiable population) of δ /year and recruitment/immigration/mark-change (rate at which marked animals join the identifiable population) of $r + \delta$ /year; and population size N in the midpoint of the study period (1990). Parameters (N , δ , r) were chosen to maximize the likelihood of the mark-recapture data under the model, as described by Jolly (1979). For a given N , δ , and r , the likelihood for years $i = 1, \dots, I$, was calculated from

$$L = \prod_{i=1}^I (1 - \delta)^{z_i + m_i} \cdot (1 - p_i)^{z_i} \cdot p_i^{m_i} \cdot q_i^{s_i}, \quad (1)$$

where

$$q_i = \sum_{j=i+1}^I (1 - \delta)^{j-i-1} \cdot \delta \cdot \left(\prod_{k=i+1}^j (1 - p_k) \right) + (1 - \delta)^{I-i} \cdot \left(\prod_{k=i+1}^I (1 - p_k) \right);$$

q_i is the probability of not being photographed after year i ; $p_i (= n_i / (N \cdot e^{r(i-1990)}))$ is the probability of being photographed in year i ; n_i is the number of individuals photographed in year i ; m_i is the number of individuals photographed in year i as well as in a previous year; s_i is the number of individuals photographed in year i but not later; and z_i is the number of individuals photographed both before and after year i but not during year i .

Because Galápagos sperm whales travel in permanent units and are thus not encountered independently, the standard methods used for estimating the precision of mark-recapture estimates (Buckland & Garthwaite 1991) are not applicable. Instead we used a modified version of the parametric bootstrap method described by Whitehead et al. (1992). Populations of female and immature sperm whales that visit the Galápagos were simulated on a computer. For each of 1000 simulations, a population of size $N \cdot e^{r(1985-1990)}$ (i.e., the number of animals in 1985) was created, using values of N and r as estimated by maximum likelihood, with likelihood calculated as in equation 1. These individuals were allocated to permanent units using the actual distribution of estimated sizes of permanent units from the Galápagos population (J. Christal and H. Whitehead unpublished data). The mean size of these permanent units was 7.5 animals (SD 5.3). Because the maximum likelihood estimate suggested that the population was decreasing (negative r), in the simulations permanent units left the population at a rate $-r$ /year. Because most of the rate of population change is thought to be due to the migration of permanent units, rather than the death of individuals, we randomly re-

moved units rather than individuals. This is a conservative procedure: removing individuals rather than units gives narrower confidence intervals. To simulate mortality and birth, individual animals were replaced by new individuals (in the same unit) at an instantaneous rate of $r + \delta/\text{year}$ (r and δ as estimated by maximum likelihood).

During the simulations, in each study year, units were chosen randomly, with replacement, and individuals from these units were identified during each encounter with probability 0.585 (as estimated by Whitehead et al. [1992] from the rate of sighting of individuals during months in which other members of their permanent units were identified) until the actual number of individuals identified during the year had been identified. This produced a simulated data set of identifications collected in each year. For each simulation run, estimates of the parameters N , r , and δ were calculated using maximum likelihood (equation 1), and these were used to estimate confidence intervals for parameters and to check for bias.

The principal assumptions of the method are (1) in any year all animals in the population had the same probability of being identified; (2) identification did not affect the probability of identification in subsequent years; (3) encounters with permanent units were independent; (4) no misidentifications were made; (5) individuals all had the same rates of mortality/emigration/mark-change (δ); and (6) the rate of mortality/emigration/mark-change (δ) and rate of change of population size (r) were constant through time.

The effects of violations of assumptions 1–4 were examined by Whitehead et al. (1992), using data up to 1989, and none seemed serious. Probably the most important assumption is that all animals in the population were equally identifiable in each year (assumption 1). Heterogeneity in identification rates can lead to substantial negative bias in mark-recapture population estimates (Hammond 1990). Heterogeneity of identification could be caused by consistent differences between animals in their pattern of use of Galápagos waters, their behavior when near our research vessel, or their identifiability from photographs of a particular quality (although our use of only high quality photographs from which virtually all animals can be identified should have eliminated this factor). We checked for heterogeneity by examining the residual differences between the observed and the expected (using the fitted model) number of individuals with each identification history (Fig. 2), as suggested by Cormack (1985). Heterogeneity is indicated if residuals are high for identification histories with many and few identifications, showing that more individuals than expected were identified many times and few times. Thus, when standardized residuals (after fitting the model) in the number of individuals with each identification history are plotted against the number of years animals with that history were identified, heterogeneity of iden-

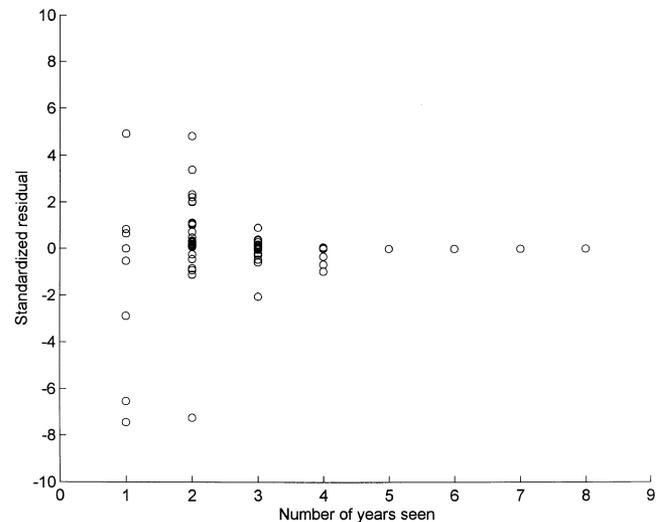


Figure 2. Standardized residuals between observed and expected (using best fit of model) numbers of individuals with each identification history plotted against the number of years individuals with that identification history were sighted.

tification is indicated by a “U-shaped” pattern (e.g., Hammond 1990). With our Galápagos sperm whale data there is no sign of such a configuration (Fig. 2). The relatively large amplitude ($> \sim 3$) of some standardized residuals can be explained by the non-independence of members of permanent units, which will tend to have the same identification histories. Important failures of assumption 5 would also produce a U-shaped pattern in Fig. 2.

Some features of the data (e.g., a peak in apparent numbers in 1989) suggest that assumption 6, the constancy of rates of population change and mortality/emigration/mark-change through time, is not strictly valid. However we expect that the results of the population analysis will approximate the average values of the parameters over the study period, and this is borne out by comparing the estimates of population size and rate of change with the mean values from a less restrictive Jolly-Seber model.

A null model, that the rate of change of population size was zero, was tested by estimating N and δ with r constrained to be zero and then running the simulation program 1000 times with these values of N and δ and $r = 0$. The distribution of the estimated values of r was compared with that estimated from the real data with the unconstrained model.

Population estimates for some study years were also calculated using the Jolly-Seber method (Seber 1982), which permits immigration/birth numbers and emigration/death rates to vary between sampling intervals (thereby eliminating assumption 6). No estimates were calculated for 1985, 1988, or 1995 because there were insufficient animals identified in these years as well as in

previous or subsequent years. No confidence intervals were calculated for these estimates because the permanent units in which female and immature sperm whales travel invalidate the standard methods of estimating error from the Jolly-Seber model. However errors in the Jolly-Seber estimates will generally be at least as large as that from the more restrictive model with assumed constant mortality/emigration/mark-change and recruitment/immigration/mark-change (Fig. 3).

Results

Ranging

Our knowledge of the ranging behavior of female and immature Galápagos sperm whales is summarized in Fig. 1. This is based on the results of Dufault and Whitehead (1995b), with a few more recent additions. Galápagos sperm whales have been known to visit the waters off mainland Ecuador, northern Peru, and the Gulf of Panama. No Galápagos identification photographs match those taken off southern and central Peru and Chile (110 individuals) or the western Pacific (100 individuals). Off mainland Ecuador and northern Peru, the Galápagos animals are sympatric with animals that do not visit the Galápagos (Dufault & Whitehead 1995b). This suggests that, over periods of a few years, the ranges of female and immature sperm whales that visit the Galápagos span approximately 1000 km.

Population Size and Rate of Change

The likelihood mark-recapture analysis shows a decrease in the Galápagos population at an estimated instanta-

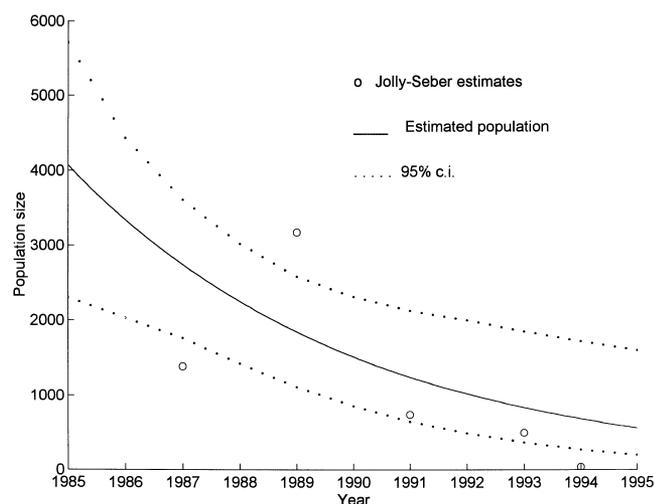


Figure 3. Estimated numbers of female and immature sperm whales visiting the Galápagos Islands with 95% confidence interval and Jolly-Seber population estimates for some study years.

neous rate of 20% per year (95% c.i. 7-32%) (Fig. 3). This rate is significantly different from 0% at $p < 0.002$ (only one estimated value of r from 1000 simulations with $r = 0$ was < -0.1975). In 1990, the midpoint of the study, the population of female and immature sperm whales using Galápagos waters was estimated at 1245 (95% c.i. 752-2205), but by 1995 there were just a few hundred. This decline is echoed by a general decline in Jolly-Seber population estimates (Fig. 3). Regressing logged Jolly-Seber estimates on year suggests a decline at a rate of 48% per year with 1035 animals present in 1990, which is consistent with the results of the restricted model when it is borne in mind that the Jolly-Seber estimates are very imprecise (having larger confidence intervals than those surrounding the estimates from the restricted model).

The rate of encountering sperm whales off the Galápagos by research vessels using standard techniques also generally declined (at a mean rate of 11%/year) during the study period (Table 2). This measure should be roughly proportional to the mean density of sperm whale aggregations in our study area around the Galápagos Islands. However, it may not be proportional to the number of animals in the Galápagos population as estimated by the mark-recapture methods if rates of entering or leaving the study area near the islands, or aggregation sizes, varied through the study period.

Mortality, Emigration, and Migrations

The combined mortality/emigration/mark-change rate was estimated to be 0.265/year (95% c.i. 0.110-0.413). Although the marks on sperm whale flukes used to identify individuals may sometimes change enough to make them unrecognizable, this seems to happen rarely (Dufault & Whitehead 1995a). Animals that change their marks this substantially will be counted as new animals, so mortality plus emigration must be greater than the rate of decrease of population size, estimated to be 0.1975/year. Thus we estimate that, on average, at least

Table 2. Rates of encountering aggregations of female and immature sperm whales and feeding success during studies off the Galápagos and mainland Ecuador and northern Peru (3°N-10°S, east of 83°W).

Year	Encounter rate/hour (SE)	Feeding success (defecations/fluke up)*
Galápagos		
1985	0.042 (0.015)	0.062
1987	0.039 (0.006)	0.021
1989	0.081 (0.023)	0.156
1991	0.012 (0.005)	0.087
1992	0.011 (0.011)	—
1995	0.027 (0.008)	0.211
Mainland		
1991	0.021 (0.007)	0.058
1993	0.031 (0.015)	0.365

*Defecation rates from Whitehead (1996).

20% of the Galápagos population were dying or emigrating each year.

Eighty-four identified individual female and immature sperm whales are known to have migrated from the Galápagos to the waters off the mainland, but none have been identified near the Galápagos following identification off the mainland (Fig. 1). Migration rates in both directions estimated from the photoidentification data were imprecise (because of low rates of sampling off the Galápagos following that off the mainland and other reasons), and the estimates were not significantly ($p < 0.05$) different from one another. However, the best estimate for migrations from the mainland to the Galápagos is 0.0/year, and that from the Galápagos to the mainland (estimated minimum of 0.075/year) is consistent with the hypothesis that much of the decline in Galápagos population size is due to migration to waters off the mainland.

Recruitment

The mean (over major studies) proportion of first-year calves relative to females and immatures sighted off the Galápagos was 0.037 calves/individual/year (SE 0.011). Richard et al. (1996), using molecular sexing, estimated that 79% of the females and immatures off Ecuador were female (the rest being immature males). If this is also true for Galápagos, and assuming an equal sex ratio at birth, then the reproductive rate is about 0.046 calves/female/year.

An alternative, but less precise, estimate of recruitment rate is the difference between the estimated mortality + emigration rate and the rate of decrease of population size from the mark recapture analysis (although this also includes rate of mark change). This has a mean of 0.067 calves/individual/year (SE 0.047; 95% c.i. -0.0154-0.1658, from results of simulations).

Discussion

There are two principal results of our analysis. The population of female and immature sperm whales visiting the waters off the Galápagos Islands fell at a rate of approximately 20% per year between 1985 and 1995, and the recruitment rate of the whales both off the Galápagos (about 0.05 calves/female/year) and mainland Ecuador is very low.

These recruitment rates are compared with observations of sperm whales in other parts of the world and predictions from the Sperm Whale Model of the Scientific Committee of the International Whaling Commission in Table 3. The rates predicted by this model are largely based on the extensive and quite reliable data set on pregnancy rates from analyses of sperm whale ovaries summarized by Best et al. (1984). The more recent

Table 3. Observed and expected proportions of sperm whale calves.

Study area	First-year calves (SE) ^a	
	Females and immatures	Source
Galápagos	0.037 (0.011)	this study
Mainland Ecuador	0.019	Kahn et al. 1993
Seychelles Islands	0.089 (0.053)	Kahn et al. 1993
Sri Lanka	0.126	Gordon 1987
Expected ^b		
Unexploited	0.098	
Exploited	0.110	

^aStandard errors are given where available and reasonably reliable.

^bCalculated using the population parameters used by the Scientific Committee of the International Whaling Commission (International Whaling Commission 1982: age of first conception 10 years; natural mortality 0.055/year; calf mortality 0.093/year; pregnancy rate 0.20/year [unexploited], 0.25/year [exploited]; and an age of dispersal of immature males of 6 years [Best 1979; Richard et al. 1996]), assuming equal mortality for young males and females of the same age and an equal sex-ratio at birth.

estimates from observations of living animals in the Indian Ocean given in Table 3 have variable reliability, but indicate substantially higher calving rates than off the Galápagos and Ecuador. The Galápagos calving rate (about 0.05 calves/female/year) is also low compared to those measured from species with similar life history parameters, such as the 0.09 calves/female/year calculated for the female resident killer whales (*Orcinus orca*) near Vancouver Island (Olesiuk et al. 1990).

For a population to have stable or increasing numbers with a recruitment rate of 0.05 calves/female/yr, mean female mortality must be less than 0.025/year (because the sex ratio at birth is nearly 0.5 [Best et al. 1984]). However both the International Whaling Commission's (1982) estimate (0.055/year) and ours (≥ 0.20 /year including migration) are substantially greater than this. Thus the calving rate that we observe is unlikely to be sustainable. A population declining at 20% per year with unsustainable recruitment is in severe difficulty. Why is the Galápagos population in this situation?

Sperm whales off the Galápagos do not appear to be subject to the most common factors that threaten some cetacean populations (Reeves & Leatherwood 1994). There has been no indication of whaling in the area between 1985-1995. Because shipping activity is low, whales are unlikely to be struck by ships. Drift nets and gill nets are also uncommon around the islands, although, of 20 sperm whales found dead on the mainland of Ecuador between 1987-1994, 11 showed evidence of interactions with fishing gear (Haase & Félix 1994). In the Galápagos region there are no known major sources of the types of chemical pollutant known to cause reproductive failure or mortality in marine mammals (Johnston et al. 1996). Preliminary data suggest that cytochrome P4501A induction in Galápagos sperm whale blubber endothelia is low as compared to mysticete and odontocete species from the Northwestern Atlantic, indicating

little circulation of planar halogenated and polynuclear aromatic hydrocarbons and, thus, low levels of these potentially detrimental classes of pollutant (M. J. Moore, personal communication). The Galápagos animals do not appear to be poorly nourished, and feeding success has been comparable to that found elsewhere in the South Pacific, in at least some years between 1985-1995 (Whitehead 1996; Table 2). There are no indications of disease in the population, although this cannot be ruled out.

In addition to the lack of any obvious cause of high mortality, there is no evidence of substantial numbers of sperm whales dying in the area. G. Merlen (personal communication), an experienced naturalist, who has lived in the Galápagos throughout our study period and has a particular interest in sperm whales, reports knowing of just two dead animals in the period 1985-1995.

The lack of any obvious threat, or substantial mortality, around the Galápagos Islands suggests that the annual disappearance of about 20% of the animals is due to emigration. The many migrations of identified animals to the waters off mainland America and the lack of any returns support this (although estimated migration rates to and from the mainland were not significantly different). A transect across the equatorial Pacific in 1992 found very few animals in the principal historical sperm whale hunting grounds along and near the equator to the west of the Galápagos (Jaquet & Whitehead 1996). This indicates that the migration from Galápagos waters was principally eastward, although results from a single transect must be treated cautiously.

The lowered sperm whale density in mainland waters caused by past whaling (possibly augmented by current by-catch [Haase & Félix 1994]) should generally give whales in mainland waters higher feeding success. Our rather sparse data is somewhat equivocal on this point, indicating moderate feeding success off the mainland in 1991 and very high success in 1993 (Table 2). Over time scales of hours to days, sperm whales move from areas where their feeding success is low, but remain where it is high (Whitehead 1996).

In addition to the lowered densities off the mainland caused by whaling, another possible reason for the differential desirability of mainland waters might be the increase in abundance off Peru of jumbo squid (*Dosidicus gigas*), which has been observed during the study period (FAO 1980-1990). Jumbo squid are an important food of sperm whales (Clarke et al. 1988).

The dynamic geography of sperm whales in the eastern tropical Pacific can be illustrated schematically using basin theory as developed by MacCall (1990). In each of the three plots in Fig. 4 an approximation of the resource suitability for sperm whales (as suggested by the charts of sperm whale kills presented by Townsend [1935]) is plotted against longitude across the eastern tropical Pacific. Resource suitability is plotted downwards, with a possible distribution of relative sperm

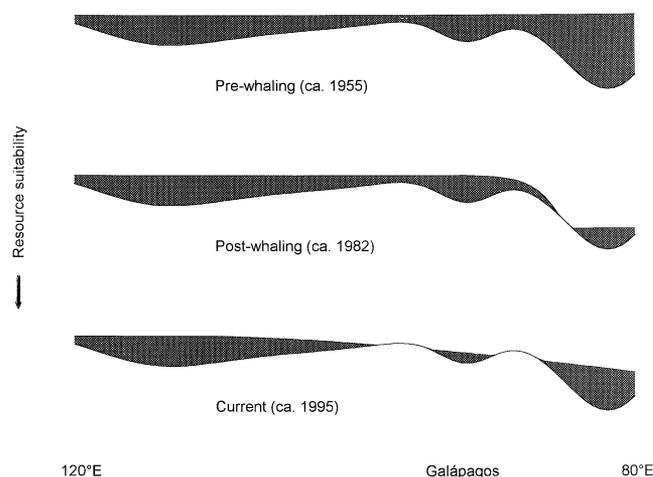


Figure 4. Visualization of the dynamic geography of sperm whale populations of the eastern tropical Pacific from 1955-1990 using basin theory (MacCall 1990). The lower curve in each of the three plots represents an approximation of the density of resources available to sperm whales at different longitudes across the eastern tropical Pacific and the height of the shaded area above this curve indicates the density of sperm whales.

whale density represented above this curve by a shaded area. With density-dependent habitat selection, an equilibrium population would be expected to fill this basin as if it were a liquid under the influence of gravity (MacCall 1990), a pattern indicated in the upper plot of Fig. 4 representing a time before the start of substantial whaling off the mainland. With intense whaling off Peru, sperm whale density in the vicinity falls (middle plot of Fig. 4). After the end of whaling, the whales gradually redistribute themselves, causing dramatic declines in abundance off the Galápagos (lower plot of Fig. 4).

It may be possible to model the dynamics of Pacific sperm whales quantitatively using basin theory, although this would be a substantial undertaking. There exist, in the form of sperm whale kill distribution shown on Townsend's (1935) charts, a measure of sperm whale resource suitability which appears to be quite reliable (Whitehead & Jaquet 1996) as well as results on sperm whale movements in relation to feeding success (Whitehead 1996) and catch statistics (collated by the International Whaling Commission). Such modeling would be quite complex, but the dynamic geographic approach of basin theory might be more successful than previous models (e.g., International Whaling Commission 1982) which assume static well-defined "stocks."

Possible causes of very few young calves being found in a population include poor nutrition, disease, and pollutant loads, which, with the possible but unlikely exception of disease, do not seem to apply to the Galápagos animals. There could be very substantial post-natal

mortality, perhaps from predation, although we have no evidence for this.

Probably the most feasible explanation for the poor reproductive rate of the Galápagos sperm whales is a low pregnancy rate due to lack of mature males and thus few conceptions. Most sexually mature, or maturing, males that are less than about 25 years old (and length about 13.5 m) are found at latitudes greater than 40°, outside the range of the majority of female groups and far from Galápagos waters (Best 1979). For this, and other reasons, it is generally thought that males younger than about 25, and smaller than about 13.5 m, take little part in breeding (Best et al. 1984).

At what we think is the height of the breeding season, large males (>12 m) constitute about 4% of the Galápagos population, well below the 15% in the catches of whalers in the area between 1830-1850 and the 16% predicted by the models of the Scientific Committee of the International Whaling Commission (Whitehead 1990, 1993).

Whalers from Peru preferentially targeted large males. Clarke et al. (1980) showed that as the proportion of males longer than 13.5 m in the catches off Peru fell (from 35% in 1958-1961 to 11% in 1975-1977), so did the pregnancy rate of females (by about 15%). In the final 3 years of Peruvian whaling (1979-1981), mature males (>13.5 m) constituted only 2% of the catch, and in the final year (1981) only one male longer than 13.5 m was caught out of a total of 225 animals (Ramirez 1989). Thus, virtually no large breeding males seem to have survived Peruvian whaling. As males do not reach these sizes until their late twenties and range widely (Best 1979), the imbalance in the sex ratio of breeding animals lingers well beyond the cessation of whaling and affects an area far larger than the whaling grounds.

Conclusion and Prospects

Our data show that between 1985-1995 there was a dramatic fall in the number of sperm whales visiting the waters off the Galápagos Islands and a very low reproductive rate. Although other explanations (such as disease or an increase in available food off the mainland during the study period) cannot definitely be ruled out, both phenomena are most obviously related to whaling which ended in 1981 and took place at least 1000 km distant. Peruvian whaling reduced sperm whale densities in the rich waters of the Humboldt Current, leaving both good feeding for animals entering these waters and providing little incentive to leave, effectively resulting in one-way migrations. Additionally, the whalers almost eliminated large breeding males from the entire region, reducing pregnancy rates in females for many years.

If we are right about the causes, then we may hope that prospects for Galápagos sperm whales will eventu-

ally improve. As animals redistribute, feeding success should equalize between the Galápagos and mainland waters (Fig. 4), so that out-migration roughly equals immigration. The number of male sperm whales in Antarctic waters (south of 60°) appears to have increased during the 1980s (Butterworth et al. 1995), and there are numbers of young males in the Galápagos/Ecuador region (Richard et al. 1996). These, if not overly threatened by fisheries by-catch or a renewed commercial hunt, should eventually start breeding, leading to an increase in pregnancy rate. However, knowledge of the population biology of sperm whales is sufficiently poor that our confidence in these optimistic predictions is not high.

If our interpretation is correct, the status of the population of sperm whales that visits the Galápagos illustrates that the negative effects of exploitation can linger a decade or more after hunting has ceased and affect very distant areas. It is also clear that a consideration of the conservation and management of wide-ranging and long-lived species like sperm whales must include large spatial and temporal scales.

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Literature Cited

- Arnborn, T. 1987. Individual identification of sperm whales. Reports of the International Whaling Commission 37:201-204.
- Best, P. B. 1979. Social organization in sperm whales, *Physeter macrocephalus*. Pages 227-289 in H. E. Winn and B. L. Olla, editors. Behavior of marine animals. Volume 3. Plenum, New York.
- Best, P. B., P. A. S. Canham, and N. Macleod. 1984. Patterns of repro-

- duction in sperm whales, *Physeter macrocephalus*. Reports of the International Whaling Commission (special issue) **8**:51-79.
- Brown, M. W., J. M. Allen, and S. D. Kraus. 1995. The designation of seasonal right whale conservation areas in the waters of Atlantic Canada. Pages 90-98 in N. L. Shackell and J. H. M. Willison, editors. Marine protected areas and sustainable fisheries. Science and Management of Marine Protected Areas Association, Wolfville, Nova Scotia.
- Buckland, S. T., and P. H. Garthwaite. 1991. Quantifying precision of mark-recapture estimates using the bootstrap and related methods. *Biometrics* **47**:255-268.
- Buckland, S. T., J. M. Breiwick, K. L. Cattanch, and J. L. Laake. 1993. Estimated population size of the California gray whale. *Marine Mammal Science* **9**:235-249.
- Butterworth, D. S., D. L. Borchers, S. Chalis, J. B. De Decker, and F. Kasamatsu. 1995. Estimates of abundance for southern hemisphere blue, fin, sei, humpback, sperm, killer and pilot whales from the 1978/79 to 1990/91 IWC/IDCR sighting survey cruises, with extrapolations to the area south of 30° for the first five species based on Japanese scouting vessel data. (Paper SC/46/SH24, submitted to the Scientific Committee of the International Whaling Commission.) Reports of the International Whaling Commission **45**:444.
- Clarke, R., A. Aguayo, and O. Paliza. 1980. Pregnancy rates of sperm whales in the southeast Pacific between 1959 and 1962 and a comparison with those from Paita, Peru between 1975 and 1977. Reports of the International Whaling Commission (special issue) **2**: 151-158.
- Clarke, R., O. Paliza, and A. Aguayo. 1988. Sperm whales of the southeast Pacific. Part IV: fatness, food and feeding. *Investigations on Cetacea* **21**:53-195.
- Colnett, J. 1798. A voyage to the South Atlantic and round Cape Horn into the Pacific Ocean, for the purpose of extending the sperm whale fisheries. W. Bennett, London.
- Cormack, R. M. 1985. Examples of the use of GLIM to analyze capture-recapture studies. Pages 243-273 in B. J. T. Morgan and P. M. North, editors. *Statistics in ornithology*. Springer-Verlag, Berlin.
- Dufault, S., and H. Whitehead. 1995a. An assessment of changes with time in the marking patterns used for photo-identification of individual sperm whales, *Physeter macrocephalus*. *Marine Mammal Science* **11**:335-343.
- Dufault, S., and H. Whitehead. 1995b. The geographic stock structure of female and immature sperm whales in the South Pacific. Reports of the International Whaling Commission **45**:401-405.
- Efron, B., and G. Gong. 1983. A leisurely look at the bootstrap, the jackknife, and cross-validation. *The American Statistician* **37**:36-48.
- FAO. 1980-1990. Yearbook of fisheries statistics. Catches and landings. Volumes 60-70. United Nations Food and Agricultural Organization, Rome.
- Gordon, J. C. D. 1987. Sperm whale groups and social behavior observed off Sri Lanka. Reports of the International Whaling Commission **37**:205-217.
- Gosho, M. E., D. W. Rice, and J. M. Breiwick. 1984. The Sperm Whale *Physeter macrocephalus*. *Marine Fisheries Review* **46**(4):54-64.
- Haase, B., and F. Félix. 1994. A note on the incidental mortality of sperm whales (*Physeter macrocephalus*) in Ecuador. Reports of the International Whaling Commission (special issue) **15**:481-483.
- Hammond, P. S. 1990. Heterogeneity in the Gulf of Maine? Estimating humpback whale population size when capture probabilities are not equal. Reports of the International Whaling Commission (special issue) **12**:135-139.
- Hope, P. L., and H. Whitehead. 1991. Sperm whales off the Galápagos Islands from 1830-50 and comparisons with modern studies. Reports of the International Whaling Commission **41**:273-286.
- International Whaling Commission. 1982. Report of the sub-committee on sperm whales. Reports of the International Whaling Commission **32**:68-86.
- Ivashin, M. V. 1978. Soviet investigations of Cetacea June 1976 to May 1977. Reports of the International Whaling Commission **28**:119-122.
- Jaquet, N., and H. Whitehead. 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. *Marine Ecology Progress Series* **135**:1-9.
- Johnston, P. A., R. L. Stringer, and D. Santillo. 1996. Incidental catches of small cetaceans. Pages 219-261 in M. P. Simmonds and J. Hutchinson, editors. *The conservation of whales and dolphins: science and practice*. Wiley, Chichester, United Kingdom.
- Jolly, G. M. 1979. A unified approach to mark-recapture stochastic models, exemplified by a constant survival rate model. Pages 277-282 in R. M. Cormack, G. P. Patil, and D. R. Robson, editors. *Sampling biological populations, statistical ecology*. Volume 5. International Cooperative Publishing House, Fairland, Maryland.
- Kahn, B., H. Whitehead, and M. Dillon. 1993. Indications of density-dependent effects from comparisons of sperm whale populations. *Marine Ecology Progress Series* **93**:1-7.
- Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature* **373**:299-302.
- MacCall, A. D. 1990. *Dynamic geography of marine fish populations*. Washington Sea Grant, University of Washington Press, Seattle.
- Olesiuk, P., M. A. Bigg, and G. M. Ellis. 1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Reports of the International Whaling Commission (special issue) **12**:209-243.
- Payne, R., V. Rowntree, J. S. Perkins, J. G. Cooke, and K. Lankester. 1990. Population size, trends and reproductive parameters of right whales (*Eubalaena australis*) off Peninsula Valdes, Argentina. Reports of the International Whaling Commission (special issue) **12**: 271-278.
- Ramirez, P. 1989. Captura de cachalote en Paita: 1976-1981. *Boletín de Lima* **63**:81-88.
- Reeves, R. R., and S. Leatherwood. 1994. *Dolphins, porpoises and whales: 1994-1998 action plan for the conservation of cetaceans*. IUCN, Gland, Switzerland.
- Rice, D. W. 1989. Sperm whale. *Physeter macrocephalus* Linnaeus, 1758. Pages 177-233 in S. H. Ridgway and R. Harrison, editors. *Handbook of marine animals*. Volume 4. Academic Press, London.
- Richard, K. R., M. C. Dillon, H. Whitehead, and J. M. Wright. 1996. Patterns of kinship in groups of free-living sperm whales (*Physeter macrocephalus*) revealed by multiple molecular genetic analyses. *Proceedings of the National Academy of Sciences of the United States of America* **93**:8792-8795.
- Seber, G. A. F. 1982. *The estimation of animal abundance and related parameters*. 2nd Edition. Griffin, London.
- Shuster, G. W. 1983. The Galápagos Islands: a preliminary study of the effects of sperm whaling on a specific whaling ground. Reports of the International Whaling Commission (special issue) **5**:81-82.
- Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. *Nature* **371**:65-66.
- Townsend, C. H. 1935. The distribution of certain whales as shown by the logbook records of American whalships. *Zoologica* **19**:1-50.
- Wade, P. R., and T. Gerrodette. 1993. Estimates of cetacean abundance and distribution in the eastern tropical Pacific. Reports of the International Whaling Commission **43**:477-493.
- Waters, S., and H. Whitehead. 1990. Population and growth parameters of Galápagos sperm whales estimated from length distributions. Reports of the International Whaling Commission **40**:225-235.
- Whitehead, H. 1990. Assessing sperm whale populations using natural markings: recent progress. Reports of the International Whaling Commission (special issue) **12**:377-382.
- Whitehead, H. 1993. The behavior of mature male sperm whales on the Galápagos breeding grounds. *Canadian Journal of Zoology* **71**: 689-699.
- Whitehead, H. 1996. Variation in the feeding success of sperm whales:

temporal scale, spatial scale and relationship to migrations. *Journal of Animal Ecology* **65**:429-438.

Whitehead, H., and N. Jaquet. 1996. Are the charts of Maury and Townsend good indicators of sperm whale distribution and seasonality? *Reports of the International Whaling Commission* **46**:643-647.

Whitehead, H., L. Weilgart, and S. Waters. 1989. Seasonality of sperm whales off the Galápagos Islands, Ecuador. *Reports of the International Whaling Commission* **39**:207-210.

Whitehead, H., S. Waters, and T. Lyrholm. 1991. Social organization in female sperm whales and their offspring: constant companions and casual acquaintances. *Behavioral Ecology and Sociobiology* **29**: 385-389.

Whitehead, H., S. Waters, and T. Lyrholm. 1992. Population structure of female and immature sperm whales (*Physeter macrocephalus*) off the Galápagos Islands. *Canadian Journal of Fisheries and Aquatic Sciences* **49**:78-84.

Appendix: analysis of migrations.

We estimated rates of migration between waters off the Galápagos and the nearby American mainland using identifications from the two regions and matches between them. We assumed no animal could be identified in both regions in the same year, that no animals migrated both ways during the 10-year study, and that all animals in region A had the same probability (c) of making a migration to region B in any year. These assumptions may not have been satisfied. However, realistic deviations from them will likely have produced only small changes in estimates of migration rates compared with their large standard errors. The expected number of animals observed migrating from area A to area B is

$$M = \sum_{i=1}^{I-1} n_{iA} \cdot \left\{ \sum_{j=i+1}^I (1-c)^{j-i-1} \cdot c \cdot \left[1 - \prod_{k=j}^I (1-p_{kB}) \right] \right\}, \quad (2)$$

where, following the notation for equation 1, n_{iA} is the number of individuals photographed in area A in year i ; p_{kB} is the probability of being

photographed in area B in year k , estimated from n_{kB}/N_{kB} ; and N_{kB} is the estimated population size in area B in year k .

We have no population estimate for the mainland region. However, an approximate lower bound (at $p = 0.05$) for the mainland population size was obtained using the lack of reidentifications between the two major study years (with 239 individuals identified in 1991, 91 in 1993), Dufault and Whitehead's (1995b) estimate of the mean number of individuals identified in a permanent unit ($G = 5.6$ animals), and binomial theory ($N_B = n_{1991}/(1-0.05^{G/n_{1993}}$). This lower bound for the mainland population is 1413 individuals and was used in equation 2 to give a lower bound for the Galápagos to mainland migration rate.

The rate of migration, c , was then estimated by finding the value of c that satisfies equation 2. For migrations from the Galápagos to the mainland, an approximate standard error for c was calculated using the jackknife procedure, omitting each year's Galápagos data in turn from equation 2 (Efron & Gong 1983). This was not possible for the mainland to Galápagos migrations because $M = 0$. However an approximate upper bound for c could be calculated because the probability that there are no observed migrations is

$$P(M=0) = \prod_{i=1}^{I-1} \left\{ 1 - \sum_{j=i+1}^I (1-c)^{j-i-1} \cdot c \cdot \left[1 - \prod_{k=j}^I (1-p_{kB}) \right] \right\}^{n_{iA}/G}.$$

The 95% upper bound for c was then that which led to $p(M=0) = 0.05$.

Using these methods, the estimated migration rate from the mainland to the Galápagos was 0.0/year (estimated 95% c.i. 0-0.105/year), and from Galápagos to the mainland 0.075/year (SE 0.055/year). This latter rate is a minimum because we only have a lower bound to the mainland population (1413 individuals). Using a mainland population of 3000 individuals, which is perhaps more realistic in light of the losses from the Galápagos region (Fig. 3), the estimated migration rate from Galápagos to the mainland becomes 0.19/year (SE 0.16/year). Thus, our data are consistent with the hypothesis that much of the decline in Galápagos population size is due to migration to waters off the mainland.

